Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

VARIATION IN THE DOG WHELK, THAIS (PURPURA AUCT.) LAPILLUS

HAROLD SELLERS COLTON

Zoological Laboratory, University of Pennsylvania

INTRODUCTION

This paper is the second of a series on the local distribution of varieties of a species of mollusk in which there is a complete mingling of the races over wide areas. It is a study of mixed populations. Gulick (1905) on the *Achatinellidae,* Pilsbry (1912) on *Liguus,* Crampton (1917) on *Partula,* and others have described the distribution of mixed colonies and pure races of mollusca separated by barriers.

Thais (Purpura) *lapillus,* the purple sea snail or dog welk, has long been distinguished as the most variable member of the littoral formation of the north European and New England coast, and indeed, with its Pacific homologue, of the littoral formation of the whole boreal region. The skeleton or shell is variable not only in color, but also in size, thickness, shape, and sculpture. The variations are so great and striking from one locality to another that if some one with a complete knowledge of the *Thais* fauna were lost in a fog and landed on the shore he could at once determine where he was by an examination of the shells on the rocks.

FACTORS INFLUENCING DISTRIBUTION

Without analysis by means of pedigree cultures we can sometimes recognize in a population two classes of variation: (1) Variations caused by the direct effect of the environment and not inherited; (2) variations caused by the chance combination of genes in the germ plasm which are inherited. We will refer to the former as environmental variations and the second as hereditary variations.

Can we distinguish environmental variations from hereditary variations by purely observational methods without recourse to experiment? This seems possible in some cases. If all members of a population differ in some character from those of another population subjected to different external conditions with no impassible barrier between, we can be pretty sure we are here dealing with an environmental character. If, on the other hand, we find individuals living side by side under the same external conditions which differ decidedly from one another in some character, we are safe to assume that we are here dealing with an hereditary character.

The present paper records an endeavor to discover the kind of variation, that is, whether the varieties are due to direct effect of environment or due to hereditary factors. Moreover, the paper will present evidence on which the distribution of certain variations can be explained.

The solving of these problems has been limited to the method of direct observation, and several factors must remain undetermined until the methods of pedigree cultures can be applied.

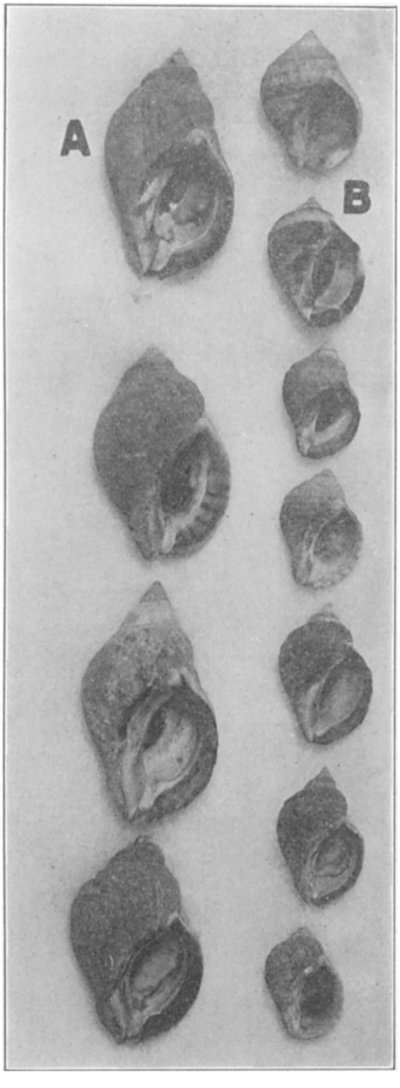

FIG. 1. Shells from the exposed coast, *B*, compared with those from sheltered harbors, *A*. An examination of large series of such shells indicates that the shape and weight of the shell is a direct reaction to the environment.

HABITS AND HABITATS

In a previous paper (Colton, 1916) the author described the life history of this form and the relations of the animal to its organic and inorganic environment. In the present case it is necessary to recall a few of the conclusions because they have a bearing on the distribution.

The habitat of *Thais* is determined by the abundance of food, freedom from enemies, and nearness of hibernating spots. In the summer *Thais* lives between the tides on rocky exposures, with the barnacle, *Balanus balanoides,* or the mussel, *Mytillus edulis,* forming the chief foods. In places where enemies in the form of fish and birds are destructive *Thais* takes refuge in deep cracks in the rocks. Moreover, on rocks far from the water at low tide, such as in coves, even with food in abundance *Thais* is not found. Coves which freeze up in the winter time are not fit habitats for the welk. This means that the distribution of *Thais* is limited by food, enemies, and topography.

The normal dispersal of *Thais* is limited to its ability to crawl. At no time in its life history does it have a pelagic stage. As soon as the young hatch they hide in cracks in the rocks, where, feeding on mussel fry, they grow to adults. It is conceivable that waves sometimes dislodge them and roll them some distance; yet normally the evidence points to their travelling in their lifetime but a hundred feet or so from the place where the eggs were laid. Yet the same varieties are found on both sides of the Atlantic Ocean.

VARIETIES OF *Thais*

The conspicuous variations in *Thais* are all concerned with the shell: shape, size, sculpture, and color. These variations in the shell, of course, are reflections of variations in the cells of the mantle which secretes the shell. The spire may be tall or short; the size is large in some habitats and small in others; the shell surface may be smooth or it may have ten distinct ridges. In some cases alternate ridges become reduced or obliterated, giving the shell six distinct ridges (figure 4). The most striking variation of all is one called *imbricata,* in which the ten ridges become fluted. Experience seems to show that all of these varieties grade into one another, but the extremes are so striking that it is a wonder enthusiastic individuals have not given them appropriate names.

INFLUENCE OF EXPOSURE ON SIZE OF SHELL AND WIDTH OF APERTURE

Shells collected from an exposed coast subject to the pounding of the surf are all small and rather thin. Those collected from stations with plenty of food in sheltered bays are large and strong (figure 1). In the former case the aperture is relatively wide (ratio, height to width $= 1.32 \pm .004$); in the latter case the aperture is relatively narrow (ratio, height to width $= 1.70 \pm$

.009). The greater area of the foot (aperture) of those exposed to the surf is a direct reaction to the environment in preventing the animal from being destroyed by the surf. Since there is no overlapping of these characters, it is evident that we are here dealing with the direct effects of environment.

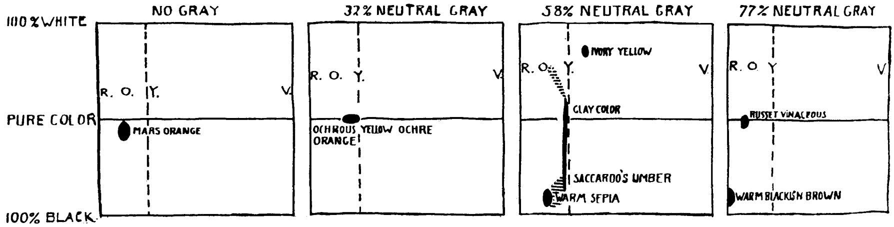

FIG. 2. The black spots indicate the distribution of the colors of *Thais lapillus* on the color chart of Ridgeway (1912). The chart seems to show that certain colors seem to offer a continuous series, but others are widely discontinuous.

R = red, O = orange, Y = yellow, V = violet, on the chart.

Shaded areas indicate where intermediates occur.

THE COLOR VARIETIES

More conspicuous than the sculpture characters are the color varieties. In describing these the author has had recourse to Ridgway's Color Standards (Ridgway, 1912).

Mars Orange. A red variety found only at St. Andrews, N. B.

Ochrous Orange and Yellow Ochre. Yellow varieties widely distributed, but rarely abundant.

Clay Color, Cinnamon, and Saccardo's Umber. Pale brownish shades widely distributed and abundant in some sites.

Warm Sepia. A purple brown, most common of the dark varieties.

Warm Blackish Brown. A dark purple, fairly common on mud flats and rare on other sites.

Russet Vinaceous. A pale purple shell very rare, absent from most sites, but forming one or two percent of the population in a few places.

Ivory Yellow. A white shell colored a pale greenish yellow within the aperture, fairly abundant.

White. Pure white even within the aperture, absent from some sites and very abundant in others.

All of these varieties are quite distinct and offer a wide distribution on the color chart (see figure 2).

Not only do differences in color exist, but also the distribution of the color on the shell takes distinct patterns. Although many of the shells are self-covered—that is, the color is uniformly distributed—yet the lip may be white or banding may be conspicuous.

The banding exists in two forms, wide bands and narrow bands, which involve the ridges on the whorls. In the wide stripe two spiral bands of white encircle the shell. The width of the stripes is somewhat variable, so that the white bands either include ridge number 4 alone or numbers 3, 4, and 5, and either number 8 alone or numbers 7 and 8.

The narrow stripe variety has every alternate ridge white, forming five to seven white bands on a colored background. In some shells these two patterns are superimposed, which results in an almost white shell with four narrow bands of color. This is shown in the following table:

Table I. *Arrangement of Color Stripes*

W = white stripe, D = dark stripe

1	2	3	4	5	6	7	8	9	10		Ridges
W	D	W	D	W	D	W	D	W	D	W	Formula for narrow stripe
D	D	W	W	W	D	D	D	W	D	D	Formula for wide stripe
W	D	W	W	W	D	W	D	W	D	W	Formula for combined effect

A white lip within the aperture is characteristic of some shells in the Mt. Desert region, while at Rye Beach, N. H., the columella is white with a conspicuous purple spot.

Distribution of Color Variations

Observation seems to show that certain color variations are independent of one another, so that many combinations are possible (Colton, 1916). Not all have been realized, however, for the possible combinations are about one thousand, and certain ones like clay color and warm sepia make up over half of the total population and but 16,000 shells have been collected.

Color Variation and Background

Since differences in color are mixed in given habitats we must consider that they are due to heredity. If this is so, how does it come about that the varieties appear in such different proportions in different stations and are not evenly distributed?

Although the yellow shells appear more abundantly on yellow-colored rocks, as was first pointed out by Blaney (1906), and the red shells have been found by the author nowhere else but on the red shales at St. Andrews, N. B.—neither at Grand Manan nor in the St. Croix River—yet the numbers are small and the backgrounds have not been carefully studied. The inference is strong, however, that natural selection has here preserved those conspicuous forms which on other backgrounds are picked off by birds at low tide and by fishes at high water.

The effect of natural selection becomes more clear when the distribution of the light individuals is contrasted with dark. Greenings Island, a small island at the mouth of Somes Sound, furnishes a good example (figure 3). The eastern end is rocky and washed by clear water. On the upper rocks, which are of black basalt, the snails feed on the white barnacles. On the lower rocks, near low tide they feed on the mussels which are black like the rocks; 61 percent on the upper rocks are light colored; 37 percent on the lower rocks are light colored. The few rocky outcrops on the western end of the island are separated from one another by mud flats. On the rocks in this region barnacles are not abundant and where present are often covered with sediment and are therefore mud colored. Here the sea snails feed mainly on the dark-colored mussels, but 3 percent to 7 percent of the shells are light colored. The proportion of dark colors evidently is determined by the background.

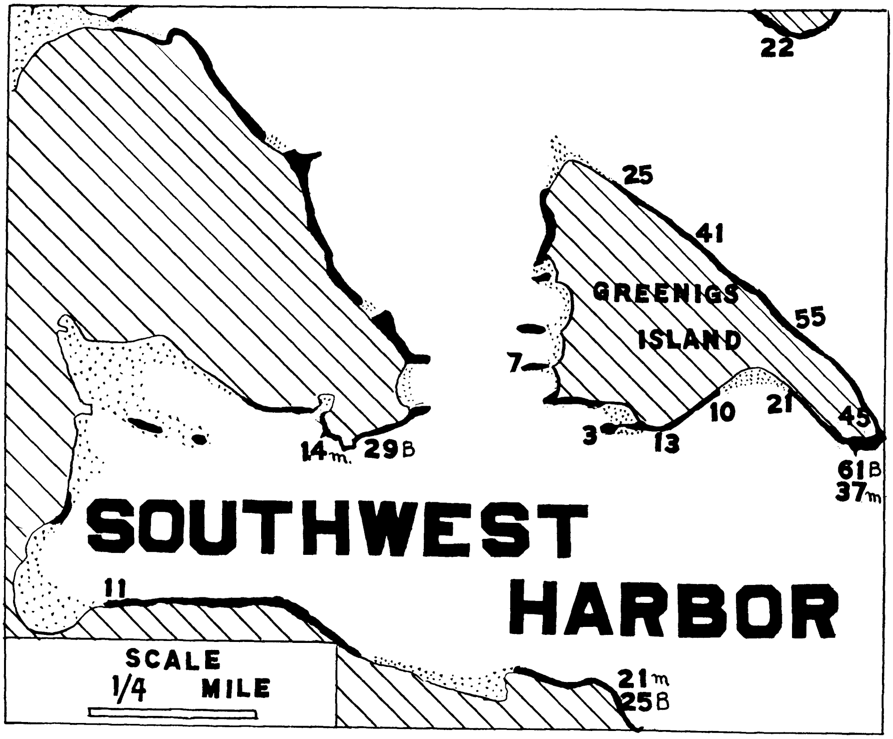

Fig. 3. Map of Greenings Island, Maine. The percentage of light colored shells is shown in figures on the various stations. On two sites collections were made close together but on different zones. "*M*" refers to *Mytilus* (mussel) zone, "*B*" to *Balanus* (barnacle) zone. The map makes clear the gradual darkening of the populations from the exposed eastern end of the island to the sheltered western end.

In other words, although the germ plasm of the populations contains the determiners for nearly all the varieties, yet a weak natural selection eliminates most of the conspicuous forms. We must assume that in some places the selection is rigorous, the conspicuous forms are all eliminated; in others it is not efficient, the conspicuous forms appear occasionally; or not acting at all, conspicuous forms are as abundant as the non-conspicuous forms. We must assume this, otherwise all conspicuous forms would disappear and the race would be homogeneous for each locality.

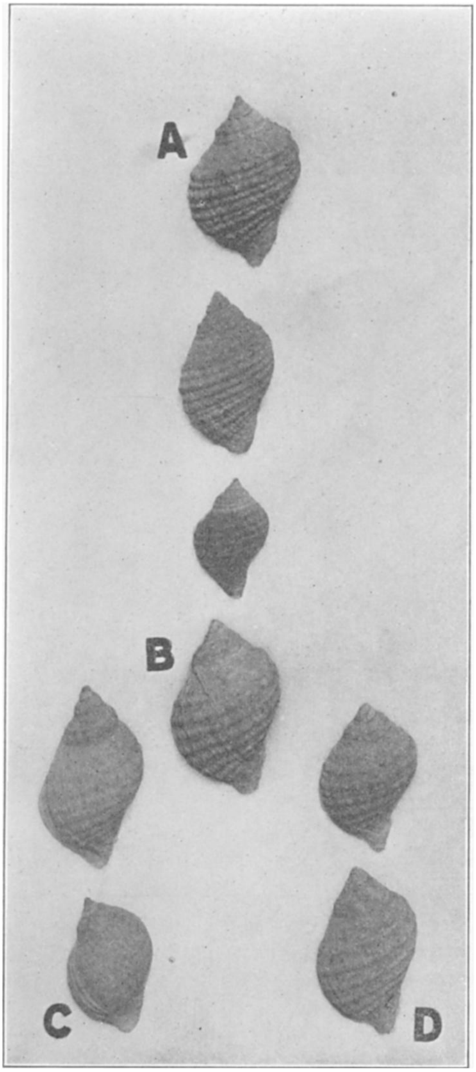

FIG. 4. A series of shells from the same station at Salisbury Cove, showing the continuous nature of the variation in sculpture. On the top we see the ten-ridged, fluted form *imbricata, A* melting into the typical *lapillus, B,* which grades into a smooth type, *C* on the one hand, and into a six-ridged type on the other.

THE VARIETY *imbricata* OF LAMARCK

The three variations in sculpture of the shell of *Thais lapillus,* smooth, ridged, and fluted, grade into one another, yet the extremes are quite distinct (figure 4). Smooth grades into ridged, ridged grades into fluted. This fluted form was described by Lamarck as a separate species, called *imbricata.* On certain rocky shores of Mt. Desert Island, Maine, it constitutes as much as 93 percent of the *Thais* fauna, and on other sites not one specimen has ever been found.

Two bays wash the shores of Mt. Desert Island, Blue Hill Bay on the west and Frenchman's Bay to the east, while the southern shore is pounded by the surf of the Gulf of Maine. An indentation of this southern shore, guarded by a number of small islands, pushes itself north ten miles in a narrow fiord, cutting Mt. Desert Island nearly in half. This fiord bears the name of Somes Sound (see figure 6).

If we study the distribution of the imbricated variety in Blue Hill Bay, we find that the fluted forms are most abundant near mud flats. Indeed, in the whole Mt. Desert region there are but two sites out of ninety where a large fluted proportion is found over half a mile from a mud flat. If perfect correlation is 1 and no correlation 0, then the correlation of the sites where *imbricata* is found to mud flats is .95. In other words, the coefficient of correlation is high.

A strip of shore a mile long was studied in detail. This strip separated two stations where the proportions of *imbricata* in the population differed greatly: 4 percent at one point and 49 percent at the other (see figure 5). It shows very beautifully the correlation between mud flats and fluting: how very few fluted forms lived on the rocks washed by the waves of the bay while in the sheltered coves nearly half the population was fluted.

Although in Blue Hill Bay, on the west of Mt. Desert Island, *imbricata* is abundant, forming 20.5 percent of the total population (4,804 individuals) and ranging from 0 percent to 96 percent of the population at different sites, depending on the proximity of mud flats; yet in Somes Sound nearby they form but 1.1 percent of the population (10,102). Eighty out of the 112 forming the 1.1 percent were from one site. Moreover, on no site does the proportion exceed 19 percent, nor is there any significant correlation between mud flats and the presence of the form. The coefficient of correlation is but .35.

This contrast between the abundance of *imbricata* in these two nearby bays is so striking because both bays have the same kind of muddy coves. Other differences that might indicate differences in physical or chemical conditions are not apparent in the fauna.

FACTORS INFLUENCING THE DISTRIBUTION OF *Thais lapillus imbricata*

As mentioned on page 146, it is possible to distinguish, in certain cases, variations caused by the direct effect of the environment from variations caused by hereditary factors. If we apply these tests to the variety *imbricata* and find that 93 percent are *imbricata* in Goose Marsh Cove, and five miles across the land at the head of Somes Harbor, just as muddy a cove, we find that .6 percent are imbricated, the fluting can not be due to the direct effect of environment. This condition is repeated over the entire area. The imbricated variation, although a case of fluctuating variation in the sense of Darwin—intergrades can be found connecting it with smooth—is clearly due to an inherited factor or factors.

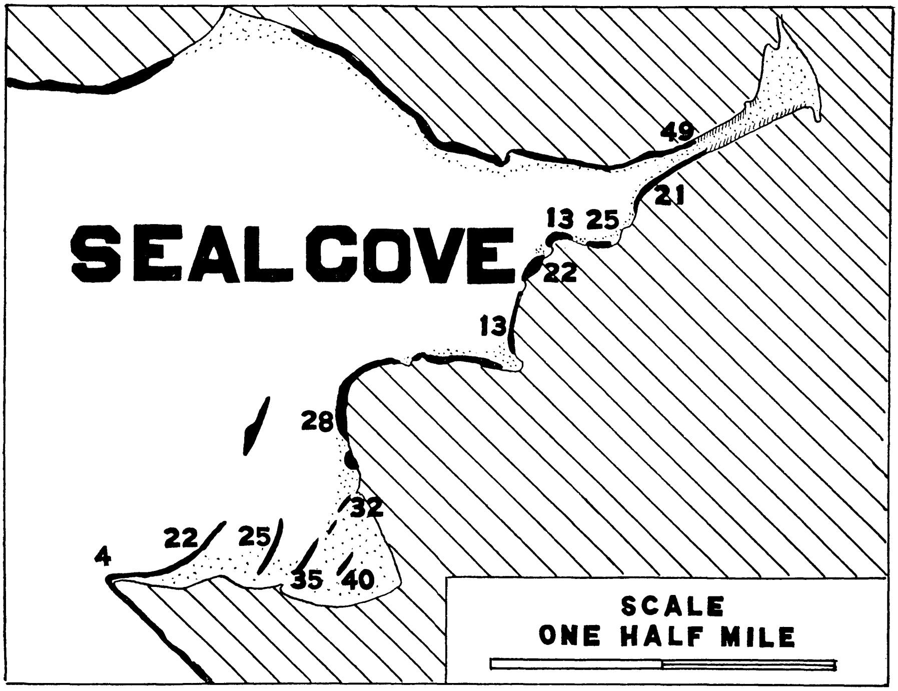

Fig. 5. On this map of Seal Cove is shown one mile of shore on which populations of *Thais* have been studied. The numbers refer to percent of *imbricata,* the form with the fluted shell. It will be noticed that on the outer point the number is but 4 percent, while at the head of the cove it rises to 4.9 percent.

The irregular distribution is apparently determined by three factors, two of which can be guessed at and the third of which is unknown.

The association of the imbricated variety with the muddy cove can be accounted for best by natural selection. These flutings on the shell accumulate sediment. Although the shell may be white, it appears as mud-colored as the rocks on which the snail crawls. The fluting comes down, therefore, to a form of protective coloration.

The almost complete absence of the imbricated form from Somes Sound and adjacent waters can only be accounted for by assuming a change of sea level in recent times. The fiord topography of the Maine coast, with the drowned valleys of the rivers; the submerged channel of Union River, which enters the northern end of Blue Hill Bay and which can be followed on the chart under the sea for fifty miles beyond its present mouth; the presence of tree stumps in situ on the beach of Greening's Island, seven or eight feet below high-water line and fifteen feet below the level of present growing trees—all of these things indicate a very recent sinking of the sea bottom.

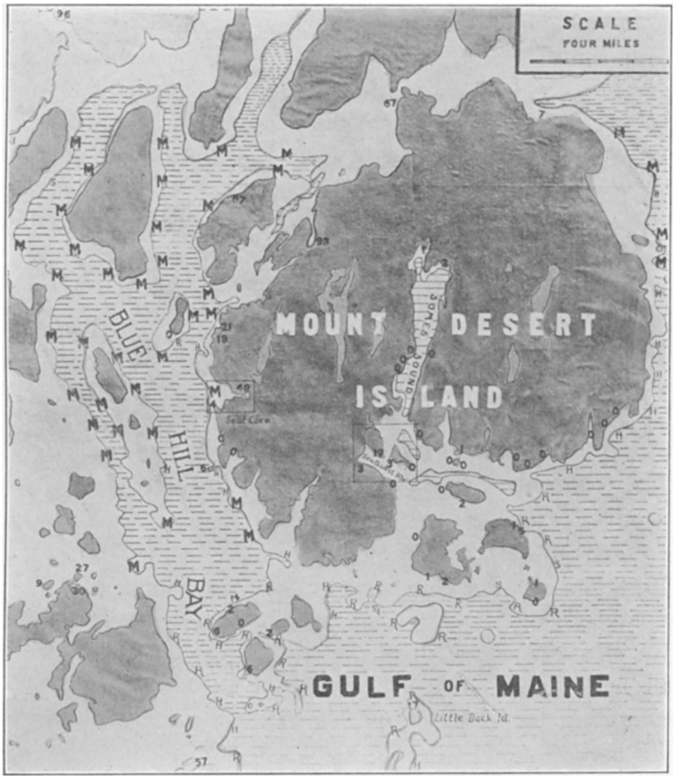

FIG. 6. A map of Mt. Desert Island, Maine, traced from a government chart. Cross-hatching shows the character of the coast line of Mt. Desert if the sea level were to fall 72 feet below its present position.

Character of the bottom at the 72 foot line: M = mud bottom, H = hard, S = sand, Sh = shell, R = rocky.

The figures give the percentage of fluted shells at each station. The striking difference between the percentage in Blue Hill Bay and Somes Sound is well brought out.

If we assume that the sea once stood at a level 72 feet below the present low-water line, the map of Mt. Desert would be quite different than at present (see figure 6). To be sure, Blue Hill Bay would still wash its western shore, which would, as now, bear muddy coves, and Frenchman's

Bay would wash the eastern margin; but the great indentation of the southern shore would not exist, and in its place would be rocky beaches, in some cases protected by a few low rocky islands, while a chain of three fresh-water lakes would lie in the present bed of Somes Sound.

If we study the present sea bottom, we find that no muddy coves could have existed on the south shore between Bass Harbor and Bar Harbor. The character of the bottom along the twelve-fathom line is shown in figure 6. If the same fauna occupied that region as now lives on the rocky southern shore of Mt. Desert, as the land sank and the sea water entered the chain of lakes it would carry with it a fauna without *imbricata*. The very few that are now found in this region and which are not associated with muddy coves could be accounted for by chance introduction by the birds that feed upon them. The 19 percent or 20 percent fluted found on the rocks of the South West Harbor steamboat wharf might have been introduced with the granite blocks which were transported in schooners from some of the upper bays during the construction of the wharf ten years ago. However, this is a mere guess. Be this as it may, the hypothesis of a change of sea level, which we know has occurred, will account for the almost total absence of *imbricata* from the shores of Somes Sound.

The fact that *Thais lapillus imbricata* appears on exposed situations on certain offshore islands (Little Duck Island 17 percent, Long Island 57 percent, and North Eddy Point on Grand Manan 95 percent) must be reserved for further study. It may be mentioned, however, that in exposed situations the imbricated forms are found only in fissures in the rocks.

Conclusion

1. An examination of a large series of *Thais* (Purpura), the purple sea snail or dog welk, from one hundred and six stations seems to indicate that variations in size and shape of shells is the result of the direct effect of environment.

2. On the other hand, variations in color and shell sculpture are due to hereditary factors.

3. The proportion of any one color variety found at a single station is determined by natural selection. More light snails are found on light environments than on dark environments.

4. If two stations offering different backgrounds are near enough together so that snails can migrate from one to the other, the proportion of a color in one station will modify the proportion in another. In other words, if a dark environment is near a white environment, then more white snails will be found in this dark site than in another with no white habitat nearby.

5. On the shores of Blue Hill Bay the fluted *Thais* (Purpura auct.) *lapillus imbricata* is in general associated with mud flats.

6. In Somes Sound the fluted form is almost entirely absent and the few

specimens that have been found are not associated necessarily with mud flats.

7. The present distribution of the imbricated form in Somes Sound can be explained by a recent change in sea level, a sinking of the land, carrying into the Somes Sound depression from the exposed coast a population free from *imbricata.* The few forms living there now can be explained as chance importations by birds and man which have not yet increased in sufficient numbers to occupy the region for which they are best adapted.

LITERATURE CITED

Blaney, Dwight

'06 List of Shell-Bearing Mollusca of Frenchman's Bay, Maine. Proc. Boston Soc. Nat. Hist., Vol. 32, No. 2.

Colton, Harold S.

'16 On Some Varieties of Thais lapillus in the Mount Desert Section, a Study of Individual Ecology. Proc. Acad. Nat. Sci. of Phila., Vol. 68.

Crampton, Henry E.

'16 Studies on the Variation, Distribution, and Evolution of the Genus Partula. Carnegie Inst. Washington.

Gulick, J. T.

'05 Evolution, Racial and Habitual. Carnegie Inst. Washington.

Pilsbry, H. A.

'12 A Study of the Variations and Zoogeography of Liguus in Florida. Jour Acad. Nat. Sci. of Phila., 2d Ser., Vol. 15.

Ridgeway, Robert

'12 Color Standards and Nomenclature. Washington, D. C.